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Published in:
Journal of Applied Ecology

DOI:
[10.1111/j.0021-8901.2004.00908.x](https://doi.org/10.1111/j.0021-8901.2004.00908.x)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2004

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Bakker, ES., Olf, H., Vandenberghe, C., De Maeyer, K., Smit, R., Gleichman, JM., & Vera, FWM. (2004). Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Applied Ecology*, 41(3), 571-582. <https://doi.org/10.1111/j.0021-8901.2004.00908.x>

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Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures

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Summary

1. Light-demanding trees and thorny shrubs in temperate plant communities may reflect adaptations to now-extinct large grazers, such as aurochs and tarpans, rendering these adaptations ecological anachronisms.

2. We explored the ecological functions of plant traits of *Quercus robur* and *Prunus spinosa* in areas grazed by cattle and horses, the domesticated descendants of aurochs and tarpans. Specifically, we tested the hypothesis that grazing induces a shifting mosaic of grassland, shrub thickets and woodlands through the key process of associational resistance: the protection of palatable young trees by thorny shrubs.

3. An enclosure experiment with transplanted *Q. robur* seedlings revealed that *Q. robur* grew best in grassland enclosures and on the edge of thorny shrub thickets, which may be viewed as an optimal balance between sufficient protection from large herbivores and sufficient light availability.

4. A cross-site comparison of four floodplain woodlands in north-western Europe showed that *Q. robur* can regenerate in the presence of large herbivores through spatial association with *P. spinosa*. However, we found that expansion of *P. spinosa* shrubs and *Q. robur* coincided with periods of low rabbit abundance and not with livestock density. From this, it appears that the process of associational resistance does not work with rabbits.

5. *Synthesis and applications.* With extensive grazing by large (domesticated) grazers in temperate floodplains, a shifting mosaic of grassland, shrubs and trees may develop that has high conservation value. Palatable, light-demanding *Q. robur* seedlings can successfully regenerate in spiny *P. spinosa* shrubs through associational resistance. This process does not offer protection from abundant small herbivores, such as rabbits, that can inhibit the recruitment of shrubs and trees in this mosaic vegetation. In floodplain meadows frequent flooding may be an efficient way to reduce rabbit populations, with dry conditions in summer and wet in winter. When floodplain meadows are combined with adjacent higher grounds, large herbivores can escape the floods through migration.

Key-words: associational resistance, cattle, grassland, grazing, mosaic, *Prunus spinosa*, *Quercus robur*, rabbit

Journal of Applied Ecology (2004) **41**, 571–582

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Introduction

Much ecological research into the relationship between organisms and environment is based on the implicit assumption that rates of environmental change, adaptation and changes in community structure are matched.

However, adaptation through natural selection is a slow process, while environmental change and species extinctions can be very rapid. Current traits that are no longer optimal for current environmental conditions, because they reflect adaptations to past environmental conditions, are called ecological anachronisms. For example, very large neotropical fruits, such as avocados *Persea* spp., are viewed as adaptations to seed dispersal by now-extinct gomphoteres and other extinct large Pleistocene herbivorous mammals (Janzen & Martin 1982). Thorny, divaricate New Zealand shrubs with small leaves are thought to have evolved in response to browsing by moas, large herbivorous birds that were driven to extinction by medieval Polynesian humans (Atkinson & Greenwood 1989; Cooper *et al.* 1993). Similarly, several species of temperate North American and European thorny shrubs may have evolved under browsing by now-extinct large Pleistocene herbivores.

These ecological anachronisms are hypotheses that are often hard to prove (Barlow 2002; Howell, Kelly & Turnbull 2002). Indirect evidence may be available from current ecological conditions in some cases, but not for interactions for which the original partner or its ecological equivalents has become extinct. In these cases only palaeo-ecological evidence can be used. Gomphoteres and moas became extinct, leaving no modern ecological proxies. However, proxies are available for the large herbivores that co-evolved with thorny shrubs in temperate regions. Large domestic herbivores, cattle and horses, domesticated from their extinct ancestors, aurochs and tarpans, make it possible to test the role of the historical ecological partners of species in current experimental research.

Temperate woodlands and meadows support a variety of thorny shrubs (such as blackthorn *Prunus spinosa* L., *Crataegus* spp. and *Rosa* spp.; nomenclature follows Van der Meijden 1990) that are light-demanding and occur mostly along forest edges (Stortelder, Schaminée & Hommel 1999). Several species of thorny shrubs exhibit a divaricate growth pattern, for example *P. spinosa* and *Crataegus monogyna* Jacq., that has been viewed as an adaptation to browsing by large herbivores (Greenwood & Atkinson 1977). This branching pattern causes a dense canopy to develop after browsing that is more difficult to penetrate, especially when the branches terminate in a sharp thorn, such as in *P. spinosa*.

In the same temperate woodlands and meadows, oaks *Quercus* spp. co-occur with these thorny shrubs. Several *Quercus* species have been reported to have difficulty in regenerating in current temperate forest reserves (Rackham 1980; Vera 2000; Johnson, Shifley & Rogers 2002; Smit 2002), which generally lack large grazers. Oaks are light-demanding trees that can germinate in the shade but need open conditions for long-term survival and growth of the seedlings (Crow 1992; Kelly 2002). We hypothesize that the traits of thorny shrubs and the recruitment strategy of more palatable woody species both may be viewed as an adaptation to now extinct partners, large grazers of the temperate zone.

Thorny shrubs and oaks could have evolved in the presence of Pleistocene and earlier fauna, as the shrub taxa *Prunus*, *Crataegus*, *Rhamnus*, *Rhus* and *Juniperus* and the taxon *Quercus* were present in Europe during the Pleistocene and even in the early Tertiary (Tallis 1991). After the extinction of most of the Pleistocene large herbivores (including many grazers, e.g. horses, bison, mastodons, mammoths, woolly rhinoceros, a ground sloth, camels and the cave bear), only aurochs, tarpans and American bison were left as large grazers in present-day temperate regions, together with several deer and antelope species and European bison as browsers/mixed feeders (Graham & Lundelius 1993; Vereshchagin & Baryshnikov 1993; Kahlke 1994). With the expansion of human settlements, aurochs and tarpans went globally extinct in 1627 (Szafer 1968; Van Vuure 2002) and the mid-nineteenth century (Vereshchagin & Baryshnikov 1993), respectively, leaving no native large bulk grazers in Europe. However, cattle and horses were introduced, and replaced the two wild ancestral species from which they were originally domesticated. They lived close to each other up to the Middle Ages (Clason 1967; Szafer 1968; Lauwerier 1988; Lebreton 1990). Therefore, the temperate woodlands and meadows with oak trees and thorny shrubs remained grazed, despite the extinction of the original partners.

In many areas, large grazers have been removed from woodlands to benefit timber production. However, in a few remaining isolated nature reserves in western Europe, so-called wood-pastures, such as the New Forest, Borkener Paradies and Junner Koeland, the natural interplay of herbivores and plant defences may be still at work. In these sites, oaks are generally surrounded by thorny shrubs (Burrichter *et al.* 1980; Pott & Hüppe 1993). It has been hypothesized that the thorny shrubs protect the palatable oak and other tree species from grazers (Vera 1997, 2000), an example of associational resistance (Olf *et al.* 1999; Callaway, Kikvidze & Kikodze 2000; Milchunas & Noy-Meir 2002). Subsequently the trees will grow and outshade the shrubs that facilitated their establishment. However, this prevents further recruitment of tree species, causing the system to return to grassland upon death of mature trees. When this cyclic succession becomes spatially asynchronized, it will result in a shifting mosaic of grassland, shrub thicket and woodland patches (Vera 1997; Olf *et al.* 1999; Vera 2000). Due to the positive correlation between heterogeneity in vegetation structure and biodiversity of, for example, insects, birds and shrubs (Cody 1975; Kollmann & Schneider 1999; Kruess & Tschardt 2002), such shifting mosaics have a high conservation value. However, the key mechanisms of this cyclic succession have not yet been experimentally proven. Associational resistance only operates when herbivores lack the ability for small-scale discrimination between palatable and unpalatable species, i.e. cannot avoid the unpalatable species when trying to eat the palatable one. The effectiveness

of the protection of palatable trees by thorny shrubs is dependent on herbivore body size; associational resistance only works against large herbivores. Small herbivores, such as rabbits and voles, will go underneath and in between thorny shrubs and consume palatable tree seedlings (Manson, Ostfeld & Canham 2001). Therefore, different-sized herbivores can have very different effects on tree recruitment.

In this study we first explored the generality of the occurrence of associational resistance in different grazed woodlands in Germany, the Netherlands and Great Britain, analysing the role of various thorny species and of different-sized herbivores. Secondly, we described the spatiotemporal dynamics of vegetation mosaics maintained by these mechanisms using historical aerial photographs. Finally, we tested the proposed protective mechanism of palatable trees by thorny shrubs in a field experiment.

Methods

STUDY SITES

Five riverine floodplains were chosen as study sites (Table 1). These were Junner Koeland, Prathoek and the Hui, along the river Overijsselse Vecht in the Netherlands (NL), the Borkener Paradies, bordering the river Ems in Germany (D), and a riverine floodplain bordering Beaulieu River, in the New Forest in the United Kingdom (UK). All five sites are nature reserves and good examples of the natural vegetation bordering most of the larger rivers in the temperate zone before canalization and intensive cultivation. They all contain hardwood forest in a grass–shrub–tree mosaic. All sites have been grazed by livestock for centuries (Burrichter *et al.* 1980; Putman 1986; Bokdam 1987; Tubbs 1997). Due to canalization of the Overijsselse Vecht and the river Ems, the floodplains are only flooded under extreme conditions, only a few times during the last century. The density and species composition of livestock at the five sites is given in Table 1. In Borkener Paradies and the Dutch sites, grazing by roe deer *Capreolus capreolus* L. was erratic and therefore not considered. European rabbits *Oryctola-*

gus cuniculus L. (hereafter referred to as rabbits) were present at all sites (Table 1).

TRANSECT SURVEYS

In Junner Koeland, Prathoek, Borkener Paradies and the New Forest, we measured shrub and tree presence along transects through the shrubs. Transects started in open grassland approximately 20 m from the edge of the shrubby area. Starting points were along a line parallel with the shrubbery, each 20 m apart. Transects ran perpendicular from the starting line into the shrubs. On the transect line sampling points were every 20 m from the starting point. A sampling plot consisted of a circle with 10-m radius from the sampling point on the transect. Shrub and tree presence were determined using the point-centred quarter method (Mueller-Dombois & Ellenberg 1974). Each circle at a sampling point was subdivided into four quarters by splitting the circle in two halves at each side of the transect line and drawing a second line perpendicular to the transect line. The presence of the nearest tree and shrub within 10 m from the sampling point was recorded for each quarter. If a quarter contained more trees or shrubs, these were ignored; if no tree or shrub was found within 10 m, a value of zero was recorded. Tree and shrub species were determined and individual diameters (trees at breast height and shrubs 20 cm above the ground) were measured and height estimated. Only shrubs and trees taller than 50 cm were recorded. Transects were sampled in spring and summer of 1998 for all sites, with 57 sampling points in Junner Koeland, 73 in Prathoek, 106 in Borkener Paradies and 75 in the New Forest. For Junner Koeland and Prathoek almost the entire woodland was covered by the transects. In Borkener Paradies more than half of the woodland patches was included in the transects. In the New Forest, the measurements were concentrated in a few hectares of woodland dominated by penduculate oak *Quercus robur* L. and ash *Fraxinus excelsior* L. on relatively rich soils close to the Beaulieu River, thus representing only a fraction of the large woodlands in the New Forest.

The association between trees and thorny shrubs was calculated by comparing the incidence of trees

Table 1. Characteristics of the study areas

Study site	Junner Koeland (NL)	Prathoek (NL)	Hui (NL)	Borkener Paradies (D)	New Forest (UK)
Coordinates	52°32'N, 6°29'E	52°31'N, 6°30'E	52°32'N, 6°35'E	52°44'N, 6°76'E	50°51'N, 1°28'W
Size (ha)	100	22	12.5	50	40000
Size of hardwood habitat (ha)	30	22	1	30	320§
Number of grazers ha ⁻¹	0.4*	0.4*	1.8*	0.4†	1.9‡
Presence of rabbits	++	++	+-	-	-

*Cattle; †cattle and horses; ‡cattle, ponies and red deer (Putman 1986).

§Only vegetation containing *P. spinosa* shrubs is considered (data from Putman 1986).

+Present; -absent; +- very low density.

occupying a sampling plot together with a thorny shrub with the incidence of plots with trees and no (thorny) shrubs, or with thorny shrubs but no trees. A χ^2 test was used to test whether trees were significantly associated with thorny shrubs. The χ^2 test was only performed when five or more trees and thorny shrubs were recorded (not necessarily in the same plots).

SHRUB EXPANSION AND TREE ESTABLISHMENT

Shrub expansion and tree establishment were studied in Junner Koeland using aerial photographs. On Junner Koeland, the shrubs consisted almost entirely of *P. spinosa*; trees were mostly *Q. robur*. On the photographs, at a scale of 1 : 2500, the *P. spinosa* shrubs and individual *Q. robur* trees were easily recognizable. Photographs from 1945 onwards were available, and photographs from 1945, 1961, 1972, 1983, 1989 and 1995 were digitized. The images were spatially referenced by matching certain landmarks that appeared on each photograph and then rescaling the photograph so that the landmarks were in exactly the same spot, to make overlays possible. Calculations of the area of shrub cover were made using IDRISI (Anonymous 1999). Periods of tree establishment were calculated using a calibration curve [age (years) = $0.7 \times \text{diameter (centimetres)} + 3.28$, linear regression: $R^2 = 0.92$, $P < 0.001$, $n = 13$]. The calibration curve was established by counts of tree rings and measured tree diameters after sampling *Q. robur* in Junner Koeland with a small core (Jorna 1984).

HERBIVORE DENSITY IN JUNNER KOELAND OVER THE LAST DECADES

Densities of cattle over the last 50 years have varied considerably, due to an increase in the size of the reserve and changing management plans. Information on cattle density at different times was obtained through personal communication with the site managers and local farmers. Rabbit counts were available from 1979 onwards. Rabbits were counted twice a year during mid-summer along a transect traversed on foot. The transect was approximately 1 km long and provided a clear view of the floodplain meadows, excluding the forest patches. Rabbits were counted using binoculars on a calm summer evening just before dusk. The higher of the two counts was taken as the number of rabbits for that year. This number gives a relative estimate of rabbit density; the transect was surveyed by one of the authors during all years. No surveys of rabbit density before 1979 were available, so we used density of rabbit burrows as counted from the aerial photographs as a relative measure of rabbit numbers. Rabbits burrowed mainly on the sandier patches, which were identifiable as clear white spots on the black and white photographs. Photographs of 1951, 1961, 1972, 1981, 1982, 1983, 1989, 1992, 1994, 1995 and 2000 were used to count burrows on the area surrounding the hardwood forest patches,

measuring 12.5 ha of grassland (of which about half was sandy and contained rabbit burrows). Burrow density was significantly correlated with the rabbit counts in the 8 years when both photographs and transect counts were available (Pearson correlation, $n = 8$, $r = 0.79$, $P = 0.02$). We therefore used burrow densities averaged over the different time periods as a measure of rabbit presence over the 50 years.

TRANSPLANTATION EXPERIMENT

A transplantation experiment was performed with 1-year-old *Q. robur* trees to study the interaction between abiotic conditions and grazing on survival and growth of oak seedlings. The experiment was performed in Junner Koeland and the Hui, to compare sites with high and low rabbit density. We purchased 432 *Q. robur* seedlings from a commercial firm in early spring 2002. The acorns were sown the previous year and the trees were delivered with a clump of soil attached to the roots; the tap root of the seedlings was cut at about 7 cm in length to make the seedling fit in a small pot. The seedling consisted of one woody stem with buds but no leaves or branches. The seedlings were stored at 5 °C until planting.

In each study site we planted 216 *Q. robur* seedlings at the end of April 2002. Seedlings were planted in four structural vegetation types: grassland, young shrub, old shrub and woodland arranged in a transect. *Prunus spinosa* was the dominant shrub species. The grassland site was located about 2–4 m from the edge of the shrubs. Young shrubs were located at the edge of the thicket and consisted of low, very spiny branches that had sprouted from rhizomes a few years previously. Old shrub was the higher and older inner part of the thicket, located 3–10 m from the young shrubs. Old shrub mostly lacked understorey, the first branches starting at about 50 cm from soil level. The woodland site was located 3–5 m from the old shrubs and consisted mainly of mature *Q. robur* trees (about 10 m tall) with very little understorey.

Three transects were established at each study site, each running through the four structural vegetation types and containing two plots in each type: one enclosure plot and one plot that was accessible to herbivores. Each plot measured 1 m² and received nine transplanted *Q. robur* seedlings. The enclosures consisted of chicken mesh wrapped around four poles to a height of 50 cm. On top of the enclosures a roof (mesh 5 × 10 cm) was constructed to prevent cattle grazing the enclosures. On 15 October 2002 all seedlings were harvested, separated into stem, current-year growth of branches and leaves, then dried at 70 °C and weighed. Live and dead trees were also determined.

We measured light availability (PAR) in the different structural vegetation types in June 2002 using a 1-m long probe containing 64 photodiodes equally spaced along its length (SunScan Canopy Analysis System; Delta-T Devices Ltd, Cambridge, UK). We took two

measurements per plot, which were averaged for further calculation.

In June 2002 we collected two soil samples per plot to measure extractable soil nitrogen. The samples were taken with a 2.5-cm diameter polyvinyl chloride tube (PVC) up to a depth of 10 cm. Mineral N was extracted from fresh soil within 24 h of sampling using 1 M KCl. The NH_4^+ and the NO_3^- contents of the soil were measured colorimetrically using a continuous flow analyser (SKALAR San plus system; SKALAR, Breda, the Netherlands).

Next to the grassland exclosures, a plot of 2×2 m was established where droppings of rabbits were counted to determine relative rabbit density. Droppings were counted every 4 weeks from April to July, and removed from the plots when counted. Rabbit density was calculated by assuming a rate of 400 droppings rabbit⁻¹ day⁻¹ (Lockley 1962).

Results

ESTABLISHMENT OF TREES

We recorded 688 trees, representing 10 species across all sites. Junner Koeland and Prathoek harboured fewer trees per sampling point than Borkener Paradies and the New Forest, and also smaller numbers of small (< 2 m) trees (Table 2). In Junner Koeland, Prathoek and Borkener Paradies, *Q. robur* was the dominant tree species (> 75% of all trees). In the New Forest *F. excelsior* (44%) was codominant with *Q. robur* (31%); together they represented 75% of all trees. The age distribution of the dominant trees (measured as stem diameter) was different for the study sites (Fig. 1; χ^2 test comparison of the number of trees 0–5 cm between the sites, New Forest values for *Q. robur* and *F. excelsior* were added: $\chi^2 = 10.2$, d.f. = 3, $P = 0.017$). In Junner Koeland and Prathoek, the oaks were approximately 20–60 cm thick, with few smaller and larger trees present. Dominant trees in Borkener Paradies and the New Forest showed a more equal distribution of trees over size classes, with many young trees. However, considering only the number of small oaks in the New Forest, there was no difference with Junner Koeland and Prathoek ($\chi^2 = 4.8$, d.f. = 2, $P = 0.09$). This might partly be a result of our methods, as we only measured the closest tree in each plot. Due to the high abundance of young *F. excelsior*

trees in the New Forest, the young *Q. robur* trees that were present, but at a lower density, were often not the closest tree and thus were not measured.

In the transects, 1054 shrubs were recorded, distributed over 20 species. Of these 20 species, seven were thorny species: *C. monogyna*, *Ilex aquifolia* L., *P. spinosa*, *Rhamnus catharticus* L., *Rosa* spp., *Rubus* spp. and *Ruscus aculeatus* L. On average 48% of the shrub species were thorny in each site (Table 2). *Prunus spinosa* was dominant ($\geq 60\%$) in Junner Koeland and Prathoek. In Borkener Paradies *P. spinosa* was codominant with *C. monogyna* (together > 60%), and in the New Forest both species shared dominance with *I. aquifolia* (together 70%). The average number of shrubs per sampling point was equal for all study sites.

ASSOCIATIONAL RESISTANCE

Young *Q. robur* trees were found associated with *P. spinosa* 49% more often than expected by chance in Borkener Paradies, the only site with enough small oak trees to test the relationship (Table 3). At this site young *Q. robur* trees were significantly associated with *P. spinosa*, whereas tall *Q. robur* trees were significantly negatively associated with *P. spinosa* in most sites. The relationship between *Q. robur* and *C. monogyna* was the other way around: a negative association was found with small trees (marginally significant) and a positive association for tall trees (Table 3). Measurements with the other thorny shrubs were pooled, as there were insufficient data available for these species. The results were similar to those for *C. monogyna*. Only in the New Forest were there enough *F. excelsior* trees to test its relationship with thorny shrubs. Young *F. excelsior* trees were not associated with *P. spinosa* shrubs, but tall trees were positively associated with *P. spinosa* shrubs (Table 3).

SHRUB EXPANSION AND TREE

ESTABLISHMENT IN JUNNER KOELAND

Expansion of *P. spinosa* shrubs in Junner Koeland varied considerably over time (Fig. 2a) and within different time periods (Fig. 3a). In some periods (e.g. 1961–72 and 1972–83) the shrubs expanded rapidly, whereas in other periods (e.g. 1945–61 and 1983–95) hardly any shrub expansion occurred. Calculation of

Table 2. Number of species and number of trees and shrubs per sampling point (maximum is 4 per sampling point, see the Methods) in four of the study sites. The Hui was not sampled because the woodland patches were too small for transect sampling

Site	Number of tree species	Number of trees	Trees < 2 m (% of total)	Trees per sampling point	Number of shrub species (% thorny)	Number of shrubs (% thorny)	Shrubs per sampling point
Junner Koeland	4	79	1 (1)	1.4	9 (44)	183 (81)	3.2
Prathoek	3	74	4 (5)	1.0	9 (44)	222 (65)	3.0
Borkener Paradies	8	262	28 (11)	2.5	12 (50)	362 (85)	3.4
New Forest	7	273	25 (9)	3.6	13 (54)	287 (96)	3.8

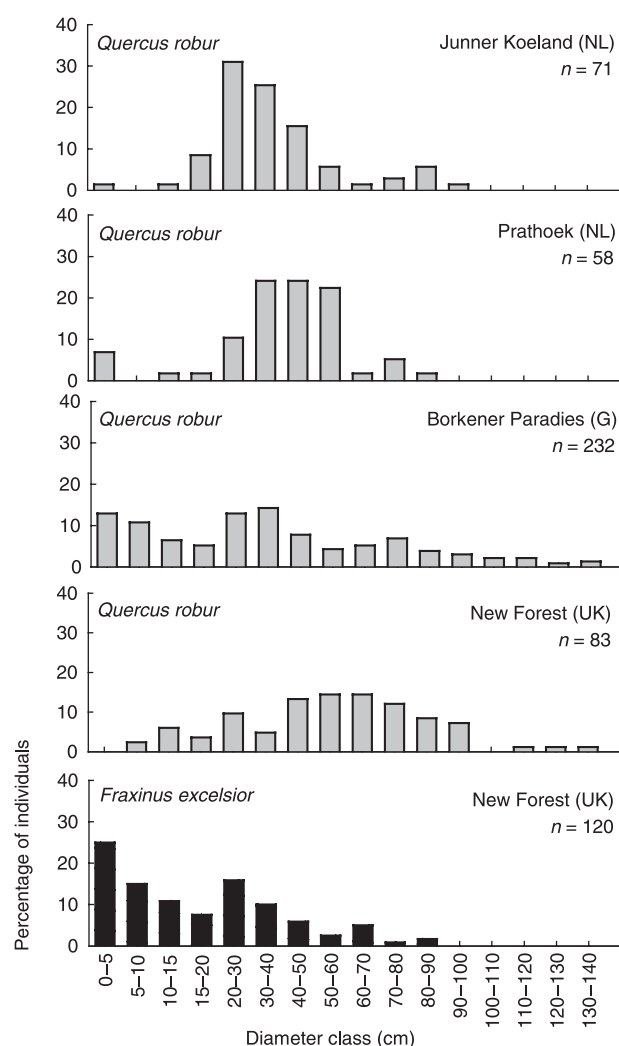


Fig. 1. Frequency distribution of *Q. robur* and *F. excelsior* stem diameters (diameter at breast height, cm) in the study sites, as percentages of the total number of individuals per tree species sampled per site (*n*).

Table 3. The association between small (< 2 m) and large trees (> 2 m) of *Q. robur* and *F. excelsior* with thorny shrubs, giving the percentage of cases in which trees were found more or less (the negative values) often than expected. The expected value is based on a random distribution of trees over quadrats containing thorny and non-thorny shrubs. Values were not determined (ND) when there were less than five trees or shrubs in a category. The association was tested using the number of quadrats where trees and shrubs (co-) occurred with a χ^2 test, * $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$

Tree species	Site	Number of trees		<i>P. spinosa</i>		<i>C. monogyna</i>		Other thorny shrubs	
		< 2 m	> 2 m	< 2 m	> 2 m	< 2 m	> 2 m	< 2 m	> 2 m
<i>Q. robur</i>	Junner Koeland	1	70	ND	-13***	ND	ND	ND	3
	Prathoek	4	54	ND	-15**	ND	4	ND	ND
	Borkener Paradies	23	211	49***	-1	-16*	10***	-4	1
	New Forest	4	84	ND	-10***	ND	13***	ND	13***
<i>F. excelsior</i>	New Forest	20	101	2	7***	4%	-2	4	-2

the establishment period of the *Q. robur* trees from the transect data resulted in a very similar establishment pattern to the increase in *P. spinosa* shrubs over time (Fig. 3b). The correlation between the number of established *Q. robur* trees and hectares of shrub expan-

sion was significant and positive (Pearson correlation, $n = 5$, $r = 0.98$, $P = 0.003$).

The cattle density declined continuously from 1945 onwards (Fig. 3c), either because of a reduction in the number of cattle or because of an enlargement of the

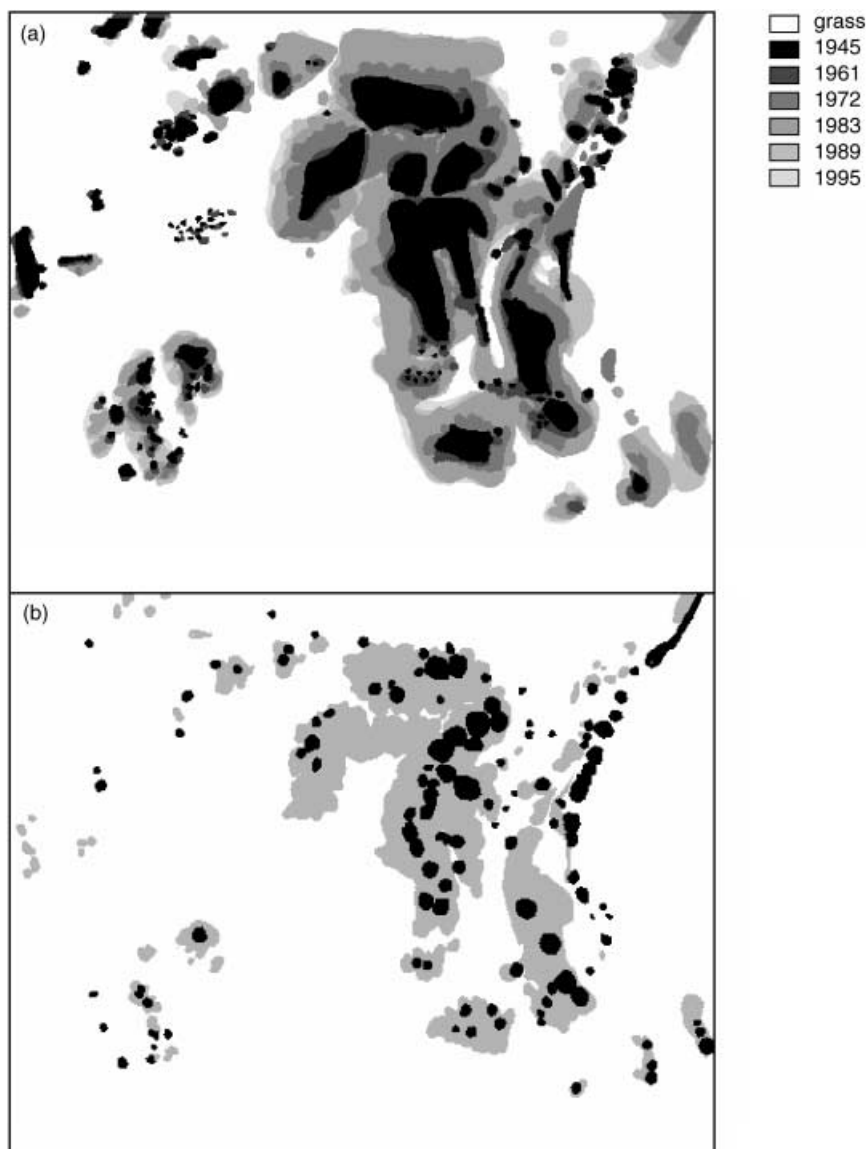


Fig. 2. Overview of the expansion of *P. spinosa* and the position of established *Q. robur* within the shrubs on Junner Koeland. The maps were created from aerial photographs. (a) Cover of *P. spinosa* shrubs in Junner Koeland from 1945 to 1995. (b) Position of *Q. robur* in 1972 indicated in black. The size of the patch represents the width of the tree canopy for each tree. The trees were mostly established within the shrubs (grey) and rarely in open grassland (white).

grazing area. Rabbit density, measured as number of burrows, increased over time (Fig. 3d).

SURVIVAL AND GROWTH OF THE TRANSPLANTED *Q. ROBUR* SEEDLINGS

Survival of the transplanted *Q. robur* trees was significantly reduced through grazing in grassland and woodland at both study sites (Fig. 4). Seedling survival in the Hui under grazing in grassland and woodland was 26% and 0%, respectively. Survival in young shrubs was about 80% and was unaffected by grazing, whereas there was 48% survival of old shrubs, in both grazed and ungrazed plots. In Junner Koeland, 85% of the transplanted *Q. robur* trees survived in the grassland enclosure and among the young shrubs, both with and without grazers. Grazing reduced survival to 26% in grassland and 11% and 15% in old shrubs and wood-

land, where survival in enclosures was already reduced to 33% and 48%, respectively.

At both study sites, the biomass of newly formed shoots was significantly suppressed under grazing in grassland and woodland (Fig. 5; Kruskal–Wallis test, the Hui: $\chi^2 = 76.7$, d.f. 7, $P < 0.001$; Junner Koeland: $\chi^2 = 104.5$, d.f. 7, $P = 0.008$, followed by Mann–Whitney *U*-tests). The young shrubs effectively protected the seedlings from grazing, resulting in no difference in shoot growth in the enclosure or under grazing. The old shrubs protected the seedlings from grazing in the Hui but not in Junner Koeland (Fig. 5). At both sites, the biomass of shoots was highest in growth among young shrubs and in the grassland enclosures.

Calculated rabbit densities were much higher in Junner Koeland (11.7 ± 2.9 rabbits $\text{ha}^{-1} \pm \text{SE}$) than in the Hui (0.8 ± 0.8 ; *t*-test, d.f. 4, $P = 0.023$).

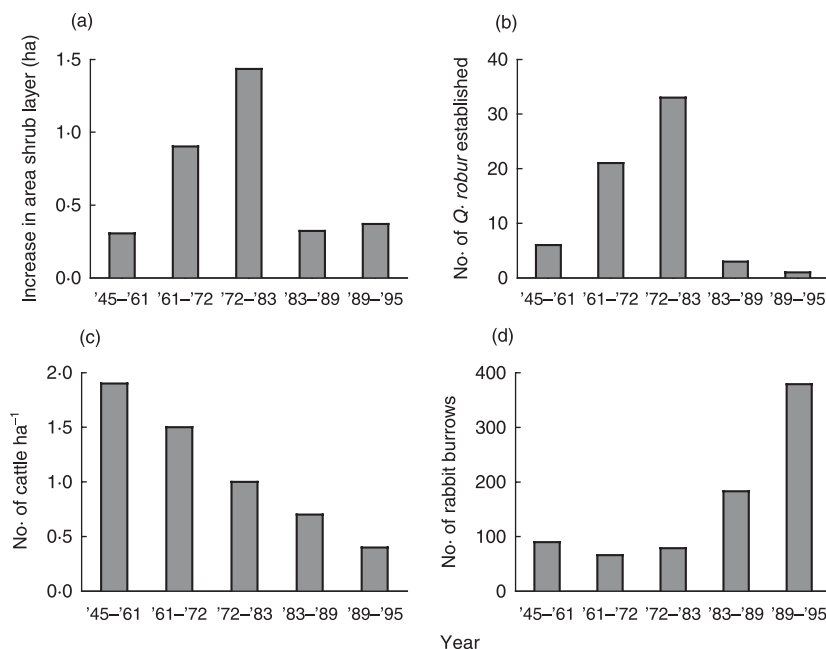


Fig. 3. The establishment of woody species and the density of herbivores during the period 1945–95 in Junner Koeland. (a) Increase of area *P. spinosa* shrubs per time period. (b) Establishment of *Q. robur* per period. (c) Cattle stocking density. (d) Relative rabbit density as the average number of burrows per period, counted from aerial photographs.

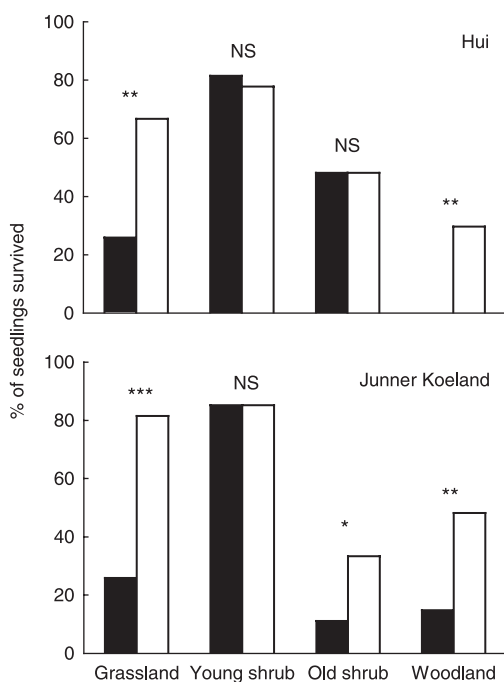


Fig. 4. Effect of grazing on the survival of transplanted *Q. robur* seedlings in different structural vegetation types ($n = 27$) in the Hui and Junner Koeland. Black bars represent the grazed seedlings, white bars the ungrazed inside the enclosure. χ^2 test, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS $P > 0.05$.

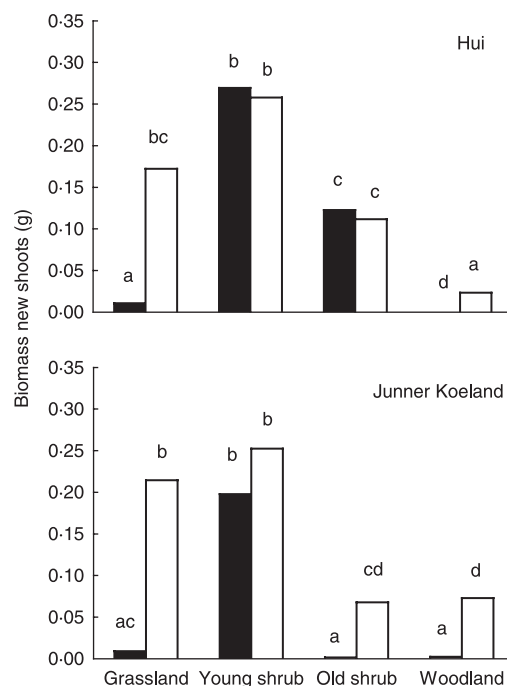


Fig. 5. Effect of grazing on biomass (g seedling⁻¹) of current year shoots of transplanted *Q. robur* seedlings in different structural vegetation types. Black bars represent the grazed seedlings, white bars the ungrazed seedlings inside the enclosure. Different letters indicate statistically different biomasses ($P < 0.05$). Data were tested with a Kruskal–Wallis test for each site, followed by Mann–Whitney U -tests.

ABIOTIC CONDITIONS IN THE DIFFERENT VEGETATION TYPES

In Junner Koeland extractable soil nitrogen increased from grassland to shrubs to woodland (Fig. 6a). This pattern was less clear in the Hui. The effect of structure type depended on the study site (ANOVA after In-

transformation: structural vegetation type \times site $F_{3,6} = 7.73$, $P = 0.017$). When soil nitrogen levels were tested per structural vegetation type per study site, values were highest in woodland and lowest in grassland and young shrubs on Junner Koeland; the old shrub plots had

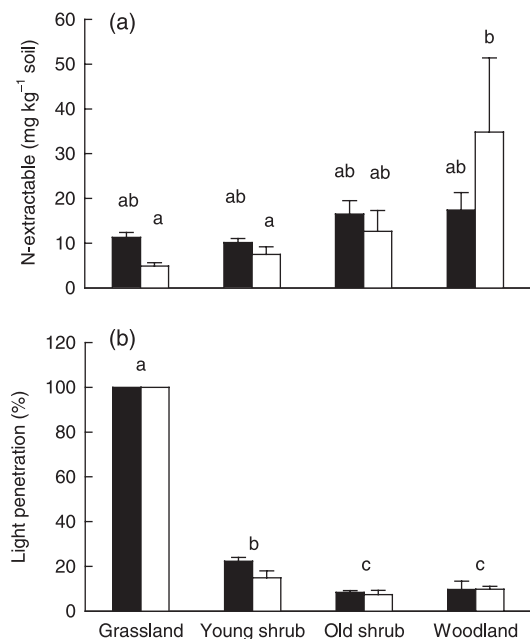


Fig. 6. Abiotic conditions in the different vegetation structural types. Black bars represent the Hui, white bars represent Junner Koeland. (a) Extractable soil N content (mg kg⁻¹) in the different structural vegetation types. Soil nitrogen level depended on the structural vegetation type and study site. Soil nitrogen levels were grouped per structural vegetation type per study site and tested with a one-way ANOVA. Different letters indicate significant differences in soil N ($P < 0.05$). (b) Light penetration at crown level of the transplanted *Q. robur* seedlings, approximately 25 cm above soil level. Light penetration is expressed as a percentage of the light level in open grassland exposed to direct irradiation. The effect of structural vegetation type was similar in both study sites. Different letters indicate significant different light levels (ANOVA, $P < 0.05$).

intermediate nitrogen levels (one-way ANOVA, $F_{7,16} = 4.44$, $P = 0.006$; Fig. 6a).

Light levels were much lower in shrubs and woodland, compared with grassland, at both study sites (Fig. 6b). In the young shrubs approximately 20% of the light was still available and in old shrubs and woodland about 10%. The effect of structural vegetation type was similar in both study sites (ANOVA after ln-transformation, site effect: $F_{1,2} = 0.39$, $P = 0.598$; structural vegetation type: $F_{3,6} = 79.32$, $P < 0.001$; site \times structural vegetation type: $F_{3,6} = 0.98$, $P = 0.463$).

Discussion

ASSOCIATIONAL RESISTANCE

Associational resistance is thought to operate in many grazed ecosystems (Vera 1997; Olff *et al.* 1999; Callaway, Kikvidze & Kikodze 2000; Rousset & Lepart 2000; Vera 2000; Milchunas & Noy-Meir 2002), yet experimental evidence is scarce (Callaway 1992; Callaway & Davis 1998). In this study we found that survival and growth of the transplanted *Q. robur* trees was severely suppressed in grassland and woodland in the presence of cattle and rabbits. Only in the young, thorny *P. spinosa*

shrubs did the transplanted *Q. robur* seedlings survive and grow equally well within and outside exclosures, showing the importance of facilitation through associational resistance. In the absence of herbivores, survival and growth was lowest in the woodland, which had the highest nitrogen levels but lowest light availability. It is probable that insufficient light was responsible for the low survival rates in woodland (Kelly 2002). The high success of young oak seedlings among young thorny shrubs thus reflects an optimal balance between sufficient protection from herbivores and sufficient light availability.

This result may explain why *Q. robur* trees were spatially associated with *P. spinosa* shrubs at a landscape scale in Junner Koeland. In this area, temporal variation in the establishment of *Q. robur* trees during the last decades coincided with expansion by *P. spinosa* shrubs. In Borkener Paradies, the occurrence of young *Q. robur* trees was positively associated with the presence of *P. spinosa* shrubs.

However, the effectiveness of associational resistance depended on the shrub species and the type of herbivore present. There was no positive association between young *Q. robur* trees and *C. monogyna* or other thorny shrubs. The different response of *P. spinosa* and *C. monogyna* may be caused by their different growth forms: *P. spinosa* is a clonal shrub that mainly spreads by root suckers, whereas *C. monogyna* is not clonal and mainly regenerates from seed. Through clonal expansion *P. spinosa* can form dense patches of young prickly ramets, which may offer better protection against grazers than the single stem of a *C. monogyna* shrub. For tall oaks (> 2 m), both positive and negative associations with shrubs were found, for example we found a negative association between tall *Q. robur* and *P. spinosa*, which was most probably due to the intolerance of *P. spinosa* for shaded conditions. In contrast, we found a positive association between tall *Q. robur* and *C. monogyna* and the other thorny shrubs at some study sites.

HERBIVORE SIZE

The effectiveness of associational resistance depended on herbivore size and herbivore foraging preferences. The transplanted *Q. robur* trees in Junner Koeland were not protected against rabbit grazing by the older *P. spinosa* shrubs, which have few spines at the bottom of their stems. Rabbits can have a strong impact on the regeneration of palatable trees through direct predation (Crawley & Long 1995) and also indirectly by eating the young stages of the protective thorny shrubs before they have developed thorns (Rackham 1980). Historical expansion patterns of *P. spinosa* shrubs in Junner Koeland showed a strong negative correlation with rabbit densities, suggesting that rabbits can inhibit clonal expansion of these shrubs. Cattle stocking rate showed no relation with shrub expansion. We therefore suggest that the main differences in tree regeneration between the four riverine floodplains that we studied is

due to differences in rabbit densities over the past 10 years rather than differences in large herbivore densities. These results are in line with the observed dynamics of woody species in Danish grasslands grazed by cattle (0.4 ha^{-1}) and sheep (0.8 ha^{-1}): *P. spinosa* and *Q. robur* were found to expand under cattle grazing but had decreased cover under sheep grazing (Buttenschön & Buttenschön 1978, 1985; Buttenschön 1988). These authors attributed this result to the higher proportion of browse in the sheep diet, and a smaller muzzle size that enables sheep to forage more selectively. Nevertheless, the process of associational resistance might operate under grazing by smaller herbivores, when the protection is offered at an appropriate scale; for example Rao *et al.* (2003) showed that browsing by mountain hares *Lepus timidus* L. on birch *Betula pubescens* L. saplings was reduced when the small trees grew in tall heather *Calluna vulgaris* L.

TREE REGENERATION IN GRASSLAND

Our results suggest that *Q. robur* regenerates better outside the woodland, i.e. at the forest edge or in grassland, than it does in the woodland interior. Oak trees grow well in grassland because there is sufficient light and they are able to resist drought by rapidly growing a tap root in the first few years (Danner & Knapp 2001). Insect herbivores and diseases, such as mildew, which are associated with the parent tree, are absent or less severe in grassland (Rackham 1980). Seed predation by rodents is also reduced in open grazed grassland compared with woodland (Jensen & Nielsen 1986; Hubbard & McPherson 1999), although typical grassland rodents, notably species of voles, can severely reduce tree establishment by grazing on saplings (Gill & Marks 1991; Manson, Ostfeld & Canham 2001).

Dispersal may be a limiting factor for shrub and tree regeneration in grassland (Herrera & Jordano 1994; Kollmann 1995). Acorns are distributed through the landscape by wood mice *Apodemus sylvaticus* L. and Eurasian jays *Garrulus glandarius* L. (Bossema 1979; Jensen & Nielsen 1986). In our study site, wood mice were mostly restricted to the woodland, but jays frequently buried acorns in open grassland (E.S. Bakker, unpublished data). Jays have also been observed to bury acorns at the fringes of thorny scrub and at the base of shrubs (Chettleburgh 1952; Bossema 1979; Vullmer & Hanstein 1995; Rousset & Lepart 2000).

ECOLOGICAL ANACHRONISMS IN WOODED PASTURES

The notion that light-demanding trees regenerate better in open areas (Vera 2000; Kuiters & Slim 2002) has major implications for landscape patterns. It implies that light-demanding trees colonize open areas, causing grassland to change to woodland, whereas woodland patches can return to grassland upon the death of trees, giving way to a dynamic process of shifting mosaics of

grassland, shrubs and trees within the landscape. Large grazers may play an important role in the dynamics of these mosaics, through maintaining open grassland areas that light-demanding trees can eventually colonize, and through intensive grazing in open patches in woodlands, which inhibits rapid reforestation of these patches (Vera 1997; Olff *et al.* 1999; Vera 2000; Gillet, Besson & Gobat 2002; Bokdam 2003). Riverine floodplains represent areas where this shifting mosaic vegetation may have operated naturally under grazing by large herbivores. Inducible mechanical defence (such as thorns and divaricate branching in trees) are thought to evolve under conditions of high resource availability, such as found on floodplain soils, because of the high carbon and nutrient requirements for these strategies (Bryant, Chapin & Klein 1983; Coley, Bryant & Chapin 1985; Grubb 1992). Large herbivores prefer drier sites with high soil nutrient availability, because these will have the highest forage quality (WallisDeVries & Schippers 1994; Olff, Ritchie & Prins 2002). The higher elevations within river floodplains are nutrient rich and dry during most of the summer. Enhanced grazing pressure may have acted to favour the evolution of thorns and divaricate branches in these habitats (Coley 1987; Myers 1987). In savannas, for example, most species of spiny shrubs and trees are found on fertile soils (Campbell 1986; Owen-Smith & Cooper 1987; Milton 1991). River floodplains have fertile soils that are favoured by herbivores and support many thorny shrub species. We suggest that the mosaic of grassland, shrubs and trees that currently exists on floodplain meadows under grazing by domestic grazers may reflect natural conditions in the past. A mosaic of grassland, shrubs and trees will harbour a great diversity of species, due to the frequent transitions between structural vegetation types (Kollmann & Schneider 1999). Currently only a few remnants of this rich system remain scattered over north-western Europe, mostly in small nature reserves. The most appropriate management of these areas may be the introduction of large grazers, particularly cattle and horses. Abundant small herbivores, such as rabbits, can inhibit the recruitment of the shrubs and trees in this mosaic vegetation. In floodplain meadows, frequent flooding may be an efficient way to reduce populations of small herbivores, with dry conditions in summer and wet in winter. Where floodplain meadows are adjacent to higher ground, large domestic herbivores can escape the floods but smaller herbivores cannot. Finally, increasing the area of small nature reserves would create more variation in grazing pressure and therefore more opportunities for the regeneration of shrubs and trees (Olff *et al.* 1999).

Acknowledgements

We thank Staatsbosbeheer (National Forest Service) for permission to perform experiments in Junner Koeland and the Hui. Jan Bokdam, Milena Blomqvist, Marike Boekhoff, Jorg Lambrechts and Jan den Ouden

provided assistance with the transect surveys. We thank Frederik Hengeveld for his help with the *Q. robur* transplantations. Johannes Kollmann and an anonymous referee made helpful comments on an earlier draft of this manuscript. This study was supported with a grant from the Netherlands Organization for Scientific Research (NWO-ALW grant no. 805-35-391).

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Received 2 July 2003; final copy received 24 February 2004